

Distinctive courtship phenotype of the Vogelkop Superb Bird-of-Paradise *Lophorina niedda* Mayr, 1930 confirms new species status

Edwin Scholes¹ and Timothy G. Laman²

¹Cornell Lab of Ornithology, Cornell University, Ithaca, NY, United States of America

²Museum of Comparative Zoology, Harvard University, Cambridge, MA, United States of America

ABSTRACT

The birds-of-paradise (Aves: Paradisaeidae) are a quintessential example of elaborate ornamental diversification among animals. Ornamental evolution in the birds-of-paradise is exemplified by the presence of a highly integrated courtship phenotype, which is the whole package of plumage ornaments, behaviors and sounds that each species uses during courtship. Characterizing a species' courtship phenotype is therefore a key part of evolutionary and taxonomic investigation in the group. With its unprecedented transmutation from bird-like form into something abstract and otherworldly, the courtship phenotype of the Superb Bird-of-Paradise, *Lophorina superba*, is one of the most remarkable of all. Recent research by [Irestedt et al. \(2017\)](#) suggests that the genus *Lophorina* is not a single species but is likely a complex of three allopatric species spanning the island of New Guinea: *L. niedda* in the Bird's Head Peninsula of the west, *L. superba* throughout the central cordillera and *L. minor* in the Papuan Peninsula of the east. Of these, *niedda* is the most phenotypically divergent with plumage traits hypothesized to possibly produce differences in ornamental appearance during display. However, the whole courtship phenotype of *niedda* has not been documented and so the actual extent of differences in ornamental appearance during courtship remain unknown. Here we analyze the first audiovisual recordings of *niedda* and compare its courtship phenotype with *superba* to test the hypothesis of potential differences in ornamental appearance. Our main goals are to: (1) provide the first description of the courtship phenotype of *niedda* in the wild, (2) determine if and how the *niedda* courtship phenotype differs from *superba* and (3) evaluate any uncovered differences in light of *niedda*'s newly recognized species status. Our secondary goal is to provide a more thorough characterization of courtship phenotype diversity within the genus *Lophorina* to facilitate future comparative study within the genus and family. Results show that the *niedda* courtship phenotype differs substantially from *superba* in numerous aspects of ornamental appearance, display behavior and sound. We highlight six key differences and conclude that the new species status of *niedda* is corroborated by the distinctly differentiated ornamental features documented here. With full species status, *niedda* becomes the fourth endemic bird-of-paradise to the Bird's Head region of Indonesian New Guinea (i.e., the Vogelkop Peninsula), a fact that underscores the importance of this region as a center of endemic biodiversity worthy of enhanced conservation protection.

Submitted 16 February 2018

Accepted 24 March 2018

Published 16 April 2018

Corresponding author
Edwin Scholes, es269@cornell.edu,
edwin.scholes@cornell.edu

Academic editor
Scott Edwards

Additional Information and
Declarations can be found on
page 20

DOI 10.7717/peerj.4621

© Copyright
2018 Scholes and Laman

Distributed under
Creative Commons CC-BY 4.0

OPEN ACCESS

Subjects Animal Behavior, Taxonomy, Zoology

Keywords Display behavior, Paradisaeidae, New Guinea, Video analysis, Birds-of-paradise

INTRODUCTION

The birds-of-paradise (Aves: Paradisaeidae) have evolved some of the most elaborate diversification in ornamental mating displays among animals (Frith & Beehler, 1998; Laman & Scholes, 2012). A key innovation behind ornamental diversification in the birds-of-paradise is the evolution of a functionally integrated *courtship phenotype* (Scholes, 2008a). A species' courtship phenotype is the whole package of plumage ornaments, behaviors and sounds used during courtship. In males, it encompasses the portion of the phenotype that is evaluated by females during courtship and in females it is the portion devoted to mate evaluation and selection (Bostwick, Harvey & Scholes, 2017). Characterizing a species' courtship phenotype is an important part of understanding evolutionary patterns and taxonomic assessment in the birds-of-paradise (Scholes, 2008b; Scholes, Beehler & Laman, 2017; Scholes, Gillis & Laman, 2017).

Among the approximately 40 species of birds-of-paradise, one of the most remarkable male courtship phenotypes is that of the Superb Bird-of-Paradise, *Lophorina superba* (Frith & Frith, 1988; Laman & Scholes, 2012). Most of what is known about courtship in *L. superba* comes from older descriptions of captive birds (Manson-Bahr, 1935; Morrison-Scott, 1936; Seth-Smith, 1936; Timmis, 1968) and two accounts of wild birds from the Adelbert Range (Frith & Frith, 1988) and the central cordillera of western Papua New Guinea (Whiteside & Feignan, 1998). From these sources and film footage of *L. superba* from near Tari, Papua New Guinea obtained for the 1996 documentary film *Attenborough in Paradise*, Frith and Beehler synthesized all knowledge of courtship and mating behavior for *L. superba* (Frith & Beehler, 1998). The picture that emerged revealed two basic types of courtship display typically given from a horizontal free fall in the forest understory: a suite of relatively simple behaviors called *initial display activity* and the iconic transmogrifying display, called the *high intensity display*, which features a highly specialized ornamental nape cape that is spread laterally to form a super black (McCoy et al., 2018) oval-shaped ruff that surrounds the entire head and upper body (Frith & Beehler, 1998). This otherworldly display has been likened in appearance to a black and blue bouncing “smiley” face-like form (Laman & Scholes, 2012).

Historically, the genus *Lophorina* has been treated as a single polytypic species with populations extending throughout mid-montane New Guinea from the Bird's Head (Vogelkop) Peninsula in the west, through all of the central cordillera and to the Papuan Peninsula in the east with isolated populations in the Adelbert Range and Huon Peninsula in the northeast (Frith & Beehler, 1998; Frith & Frith, 2009). The Bird's Head and Papuan Peninsula populations exhibit geographic variation in female head color (Cracraft, 1992; Frith & Beehler, 1998; Pratt & Beehler, 2015) and the Bird's Head population has minor variation in male ornamental plumage—i.e., no black spots on the feathers of the breast shield ornament (Cracraft, 1992; Pratt & Beehler, 2015). Recently, the Bird's

Head population has also been identified as being vocally distinct from the others, but comparative acoustic details have not yet been examined (Beehler & Pratt, 2016).

Recent analysis of DNA sequence data and external morphology from museum specimens suggest that the genus *Lophorina* is likely comprised of three species (Irestedt et al., 2017). The newly delimited species are: *L. niedda* (with subspecies *niedda* and *inopinata*) in the Bird's Head (Vogelkop) Peninsula, *L. superba* (with subspecies: *superba*, *addenda* and *latipennis*) throughout the central cordillera, Adelbert Range and Huon Peninsula, and *L. minor* in the Papuan Peninsula (Irestedt et al., 2017). Of these, *minor* is the oldest and most genetically divergent lineage, but *niedda* is the most phenotypically differentiated (Irestedt et al., 2017). For example, the breast shield feathers of male *niedda* are not as laterally extended as they are in *superba* and *minor* and the outer ornamental cape feathers of *niedda* are more elongated with outwardly-curved and narrowly rounded tips with reduced hair-like fringing (Irestedt et al., 2017). As suggested by (Irestedt et al., 2017), the plumage differences of *niedda* might be expected to produce significant differences in ornamental appearance during display and thereby further validate its newly revised species status, but the courtship phenotype of *niedda* has not been documented in the wild.

Here we analyze the first audiovisual recordings of courtship behavior in *niedda* and compare its courtship phenotype with *superba* based on analysis of audiovisual recordings from the Macaulay Library at the Cornell Lab of Ornithology and several documentary films. Our aim is threefold: (1) to provide the first description of the courtship phenotype of *niedda* in the wild, (2) test for potential differences in ornamental appearance by determining if and how the *niedda* courtship phenotype differs from *superba* and (3) evaluate any uncovered differences in light of *niedda*'s recently recognized species status. An additional goal is to provide a more thorough characterization of courtship phenotype diversity within the genus *Lophorina* to facilitate future comparative study within the genus and among species in the family.

MATERIALS & METHODS

Field observations and audiovisual recordings of two adult male *L. niedda* were made near the village of Mingre in the Arfak Mountains of West Papua, Indonesia during June–November 2016 and 2017. Multiple simultaneous recordings were made with remotely and manually operated video cameras and audio recorders from within observation blinds. Video was recorded with RED Epic-W Helium and Canon 1DX Mark II cameras fitted with a range of Canon lenses. Audio was recorded using a Marantz PMD 661 and Sennheiser microphones. Focal length, frame size and frame rates of video recordings varied according to the particular camera-lens combination used and particular environmental conditions, but ranged between 50–800 mm, 4 k–8 k and 24–240 p respectively.

For the video analysis, we screened over 200 raw field recordings using the REDCINE-X Professional and Canon EOS MOVIE Utility software applications. Clips with display behaviors were identified and analyzed frame-by-frame to identify the components of courtship described in the results. Recordings containing practice displays and displays given to females were used for the detailed analysis (Table S1). In total we analyzed 30

practice displays and 14 displays to females. Voucher recordings were archived in the biodiversity media collections of the Macaulay Library at the Cornell Lab of Ornithology (<http://www.macaulaylibrary.org>) as accession number ACC4396. Vouchers are cited in the Results using Macaulay Library catalog numbers and can be viewed and/or requested online by searching the Macaulay Library database for catalog numbers [ML487530](#) to [ML487569](#) (see also [Table S1](#)). Media can also be accessed directly using the following URL: <https://macaulaylibrary.org/asset/xxxxxx> where “x’s” are replaced with the desired catalog number.

Video frames highlighting important components of the courtship phenotype were extracted as tiff files for creating figures. Modifications to figure images included minor adjustments to improve clarity (e.g., cropping, and small adjustments in levels, brightness and contrast).

For the acoustic analysis, archival quality audio files from the Macaulay Library (44 khz, 16-bit .wav; [Table S1](#)) were analyzed with the sound analysis software package Raven Pro version 1.5 (Cornell Lab of Ornithology, Ithaca, NY, USA).

Video used for the analysis of *L. superba* came from existing archival video and sound recordings from the Macaulay Library ([Table S1](#)) of two individual adult male *superba superba* ([ML487529](#), [ML487528](#) and [ML458167](#)) and one individual adult male *superba latipennis* ([ML458001–ML458003](#)). All of the recordings with data used in the analysis are cited in the Results and can be viewed and/or requested online via the Macaulay Library database as described above.

To broaden our review of potential interspecific variation within *superba*, we also reviewed broadcast video footage obtained by film crews during the production of three documentary films: (1) *Planet Earth* (2006) produced and distributed by the BBC, (2) *Nature: Birds of the Gods* (2011) distributed by PBS, and (3) *Designed to Dance: Birds of Paradise* (2011) produced by NHK Wildlife. Through communications with the producers and/or with local informants at the filming locations, we know that all three the documentary sequences were filmed near the town of Tari in Hela Province, Papua New Guinea and therefore all represent the subspecies *L. superba addenda*. Clips containing the segments we reviewed and/or full episodes for each film can be viewed online through a variety of sources (e.g., the Planet Earth segment is viewable on the YouTube channel of BBC Earth: <https://youtu.be/nWfyw51DQfU?t=2m10s> and *Birds of the Gods* can be viewed on the Nature website: <http://www.pbs.org/wnet/nature/bird-of-the-gods-full-episode/13378/?button=fullepisode> from 40:41 to 42:58). Due to copyright restrictions, we could not include comparable images of *addenda* in our figures, but unless otherwise noted, the courtship phenotype of *addenda* was found to be identical to those of *superba* and *latipennis* documented here.

RESULTS

Initial display activity

Our analysis identified three distinct types of initial display activity in *niedda*, which broadly correspond with those of *superba*. In the order in which they occur within the

courtship sequence, they are: advertisement, horizontal and pointing displays. Each display is described in detail below. Our analysis did not identify substantial variation in the behaviors, postures and ornaments within the *superba* complex (i.e., among *s. superba*, *s. addenda* and *s. latipennis*) and so we use *latipennis* as the frame of reference to describe and illustrate the *superba* complex (but see Fig. S1 for details of *superba superba*). Although the three types of initial display activity broadly correspond with those of *superba*, our analysis found that each display of *niedda* has numerous distinctive elements.

Advertisement display

The central features of this display involve the male excitedly looking up and around from side to side (presumably for a potential mate) while repeatedly flicking his cape forward in front of his head and calling (video vouchers: *superba* ML458000 from 0:44 to end; *niedda* ML487533). Upon arrival to the fallen log used for display, the male stands in an alert upright posture with head up, bill forward and tail down (Figs. 1A & 1B and S1A). The iridescent crown feathers are pushed (anteriorly) toward the bill so that they do not visibly reflect any blue and the entire head appears black from all directions. In this configuration, the ornamental eye-spots are not visible (Figs. 1A & 1B and S1A & S1B). In *niedda*, the male typically arrives and departs from his display log by flying low through the forest understory rather than by dropping down from or flying up to the forest canopy immediately above. It is unclear if *superba* does the same with the available data.

In *superba*, the main posture of the advertisement display has the nape cape folded over the back and wings, without being spread, such that the terminal tips of the cape reach to, or extend beyond, the base of the tail completely covering the wings (Fig. 1A). In *niedda*, the configuration differs in that the cape sits spread over the upper back such that the terminal tips extend conspicuously to the sides leaving the wing tips and base of the tail uncovered (Fig. 1B).

In *superba*, the feathers of the breast shield are held close to the breast and upper body so that, for the most part, the color of the ornament is not visible, especially as viewed from above (Figs. 1A and S1A). One exception is during high-intensity calling in which case the breast is thrust forward causing the breast shield to be pushed outward and made visible (Fig. S1B). In contrast, the breast shield of *niedda* is not held as tightly against the breast and its shorter and narrower lateral tips do not fold back toward the torso as in *superba* (Fig. 1B). The terminal tips of the *niedda* breast shield curve gently outward, which makes the surface of the breast shield slightly concave (Fig. 1B). In both *superba* and *niedda*, the bright yellow color of the gape becomes visible while calling (Figs. 1A & 1B and S1B).

Beyond repeated side to side head turning, the primary movements of the display are a frequent forward “flicking” of the cape, which results from turning the head down and to the side and into a partially open wing in order to perform a rapid false wing preen motion (Figs. 1C and 1D). The extremely fast movement of the false-preen causes the cape to be quickly flicked forward over the downward turned head in a highly exaggerated and ritualized fashion. In *superba*, the cape largely retains its compact form when flicked forward whereas in *niedda*, the flicked cape is fanned out over the head (Figs. 1C and 1D).



Figure 1 Advertisement display of *superba* and *niedda*. The central features of this display involve the male excitedly looking up and around from side to side while calling and flicking the cape in front of the head. In *superba* (A), the cape is held folded over the back and wings, without being spread, such that the terminal tips of the cape reach to, or extend beyond, the base of the tail (see arrow). The feathers of the breast shield are held close to the breast so that the color of ornament is not visible. In *niedda* (B), the cape is spread widely over the upper back such that the terminal tips extend conspicuously to the sides (see arrow) leaving the wing tips and base of the tail uncovered. The breast shield is not held as tightly against the breast and its shorter and narrower lateral tips do not fold back toward the torso as in *superba*. The terminal tips of the *niedda* breast shield curve gently outward, which makes the surface of the breast shield slightly concave. The primary movement is a frequent forward “flicking” of the cape, which results from turning the head down and to the side into a partially open wing in order to perform a rapid false wing preen motion. In *superba* (C), the cape largely retains its compact form when flicked forward, whereas in *niedda* (D), the cape fans out distinctly over the head. Image credit/source: (A and C) Edwin Scholes/ML458003 and (B and D) Tim Laman/ML487533.

Full-size  DOI: [10.7717/peerj.4621/fig-1](https://doi.org/10.7717/peerj.4621/fig-1)

Horizontal display

This display is frequently interspersed throughout bouts of the advertisement display and involves the diagnostic adoption of a rigid horizontal posture with the neck outstretched, head lowered, and bill pointing forward to be in line with the body axis (video vouchers: *superba* ML458000 (from 0:33–0:44) and ML458001 (from 0:27–0:34); *niedda* ML487558 from 0:00–0:30). The tail is also lifted so that the whole body forms a horizontal line from tip of the bill to tip of the tail (Figs. 2 and S1C).

In most instances, the crown feathers are pushed forward so that the head remains all black in appearance and the ornamental eye-spots are not visible (Fig. 2). However, the eye-spots are occasionally revealed during practice displays or if the bird is about to

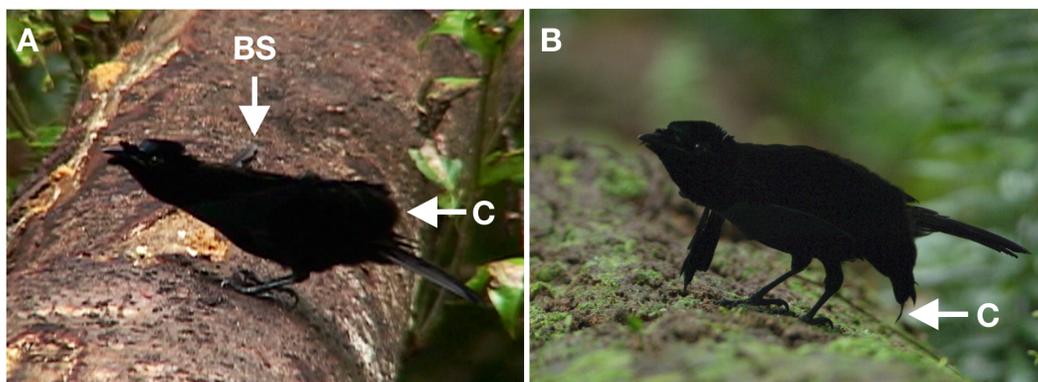


Figure 2 Horizontal display of *superba* and *niedda*. This display involves the diagnostic adoption of a low rigid horizontal posture with the neck outstretched, head lowered, bill pointing forward and tail lifted to be horizontal so that the whole body forms a horizontal line from tip of the bill to tip of the tail. Crown feathers are pushed forward so that the head remains all black in appearance and the ornamental eye-spots are not visible. In *superba* (A), the cape is folded over the back to the base of the tail and is not spread. Arrow “C” points to the terminal tips of the cape feathers. The longest feathers in the breast shield of *superba* stick out conspicuously to the sides while the central breast feathers are sleeked against the body so that no color is visible. The dark outwardly pointed tips give the appearance of being small pointy “wings” sticking out from the sides of the breast. Arrow “BS” points to the terminal tips of the breast shield feathers on the bird’s right side. In *niedda* (B), the cape is spread widely over the upper back to form a slightly raised narrow crescent with decurved “wings” spread to each side and with tips that droop to the log. Arrow “C” points to the terminal tips of the cape feathers on the bird’s right side. The breast shield of *niedda* is sleeked against the body with no color visible. Unlike the arrangement in *superba*, the longest breast shield feathers of *niedda* are not as noticeable because of how they are obscured by the wing-like position of the cape. Image credit/source: (A) Edwin Scholes/ML458003 and (B) Tim Laman/ML487563.

Full-size DOI: 10.7717/peerj.4621/fig-2

transition into the pointing display (see below), but then concealed again as the horizontal display continues or the bird ruffles its plumage and returns to a bout of advertisement display.

In *superba*, the cape is folded over the back to the base of the tail and is not spread (Figs. 2A and S1C). In a position that creates a very different appearance, the cape of *niedda* is held over the back, but spread so that it forms two decurved “wings” that emanate from each side and with tips that droop to the log (Fig. 2B). At times, the cape is partially lifted over the back so that it forms a slight arch behind the head.

In *superba*, the longest (lateral) feathers of the breast shield stick out conspicuously to the sides and the central most breast feathers are sleeked against the body so that no color is visible, especially when viewed from above (Fig. 2). Because the body is in elongated horizontal posture, only the blackish underside (ventral side) of the breast feathers project outward. The dark outwardly pointed tips give the appearance of being small pointy “wings” sticking out from the sides of the breast. In *niedda*, the breast shield is also sleeked against the body with no color visible (Fig. 2B), however unlike the arrangement in *superba*, the longest breast shield feathers do not look like “wings” because the wing-like position of the cape obscures them (Fig. 2B).

The main movement of the horizontal display is ritualized hopping “run” along the log to change position and orientation (e.g., see ML487557 from 1:16 to end and ML487563

from 0:00–0:25). The hops use both feet at the same time and are typically initiated with a quick wing-flick just prior to the first hop. Although less frequent than in advertisement display, the false wing-preens that cause frontal cape flicking are also given.

Pointing display

The final display in the initial display activity sequence begins from the posture of the horizontal display, which is the most common, or following an advertisement display vocalization. As the name suggests, the primary feature of this display involves the adoption of a ritualized pointing posture where the bill points skyward as the male's attention is oriented toward a potential, or actual, female (video vouchers: *superba* ML458002 from 0:22–0:53 and ML458003 from 0:50–0:56; *niedda* ML487538 from 0:00–0:03 and ML487540 from 2:10–2:23). In *superba*, the body is held in an upright posture, with the upper body lifted from the horizontal to be erect as if the bird is “standing at attention” (Fig. 3A). In *niedda*, body posture is more horizontal with the upper body closer to the log and the head tilted back so that the bill points upward (Figs. 3B and 4).

A key feature of this display is how the feathers of the fore crown are pushed back (posteriorly) to be flattened against forehead while the hind crown feathers remain pushed forward (anteriorly). This result of this repositioning is that the highly reflective fore crown feathers become visible, changing the appearance from all-black to an iridescent electric blue (Figs. 3 and 4). At the same time, the feathers of the narial tufts are also pushed outward from both sides of the bill, which when aligned with the blue fore crown feathers, and viewed head-on, create the highly distinctive eye-spot ornament. When visible, the eye-spots reflect so brightly relative to the super-black plumage surrounding them that they look somewhat like a pair of headlights (Figs. 3 and 4). It should also be noted that the shape of the erected narial tufts differs between *niedda* and *superba*. In *superba*, the tufts are shorter and thicker, almost wedge-shaped, and do not extend beyond the width of the head (Fig. 3A). In *niedda*, the tufts are narrow and elongate with tips that extend out beyond the width of the head (Fig. 3B).

As with the previous behaviors, the arrangement of the cape differs substantially between *superba* and *niedda*. In *superba*, the cape remains tightly folded over the back and is not noticeably spread (Fig. 3A). In *niedda*, the cape is always prominently spread broadly over the back to form the conspicuous decurved wing-like lateral protrusions that are a hallmark of the *niedda* courtship phenotype (Fig. 3B).

During the pointing display, the breast shield of *superba*, though not as outstretched as in the cape presentation display (see below), is nevertheless quite prominent with its reflective blue color visible (Figs. 3A and S1D). In *niedda*, the breast shield remains sleeked against the breast and largely invisible—its lateral tips concealed (shadowed) by the protruding “wings” of the cape—when viewed from the vantage point of an approaching female (Fig. 4).

The main movements during the pointing display involve a ritualized flapping of the cape up-and-down over the back and occasional reorientation along the log to “track” the position of a female as she moves around nearby or approaches. The details of the cape-flap differ between *superba* and *niedda*. In *superba* the cape-flap occurs when the wings are partially lifted and flicked open over the back in coordination with a quick pronounced

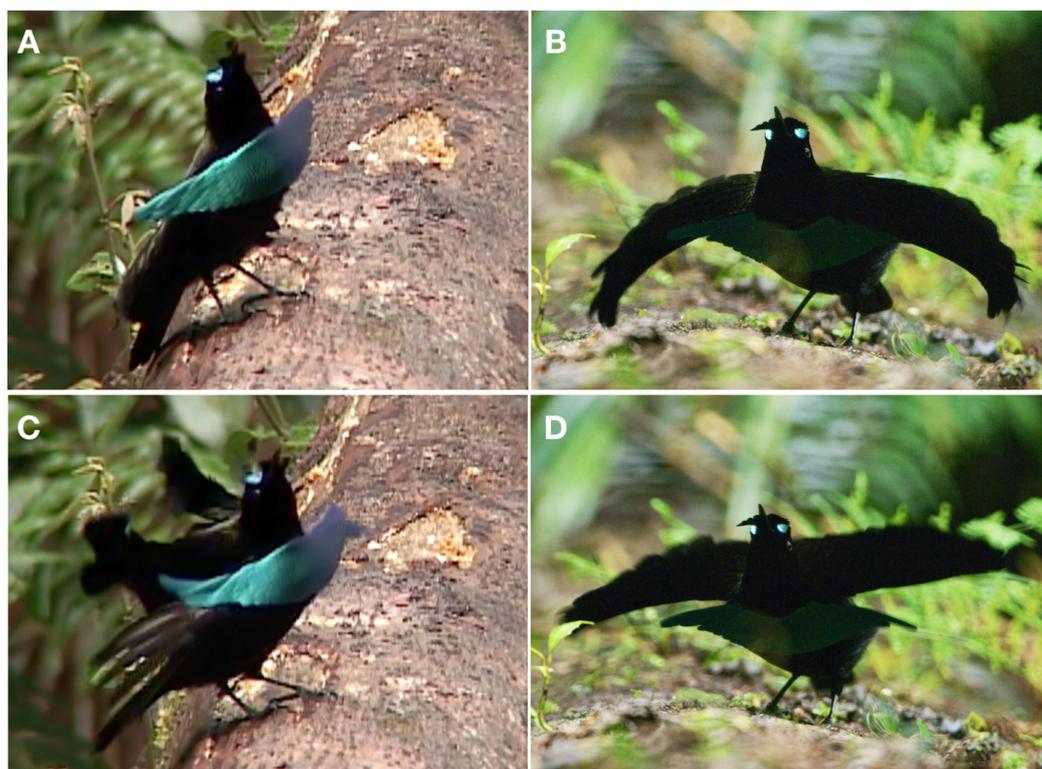


Figure 3 Pointing display of *superba* and *niedda*. This display involves a ritualized pointing posture where the bill points skyward. The feathers of the fore crown are pushed back against forehead the while the hind crown feathers remain pushed forward, which makes the reflective fore crown visible. The narial tufts are lifted outward from both sides of the bill, which creates the distinctive eye-spot ornament when aligned with the fore crown feathers and viewed head-on. In *superba* (A), the body is held upright, as if the bird is “standing at attention” with breast shield prominently displayed. Narial tufts are wedge-shaped and do not extend beyond the width of the head. The cape remains folded over the back. In *niedda* (B), the body posture is more horizontal with the head tilted back so that the bill points upward. Narial tufts are elongate with tips that extend out beyond the width of the head. The cape is spread over the back to form the conspicuous decurved wing-like protrusions, which obscure the breast shield. Movements include a ritualized flapping of the cape over the back. In *superba* (C), the cape-flap occurs when the wings are partially lifted flicked open over the back in coordination with a quick foot stomp, which causes the cape to flap up-and-down such that the terminal tips of the cape feathers rise above the height the of the head. In *niedda* (D), there is a foot stomp, but wings are only raised slightly up-and-down over the back, which causes the terminal tips of the cape feathers stay at or below the level of the head. Image credit/-source: (A and C) Edwin Scholes/ML458003 and (B and D) Tim Laman/ML487538.

Full-size DOI: 10.7717/peerj.4621/fig-3

foot stomp, which causes the cape to flap up-and-down over the back in an exaggerated way such that the terminal tips of the cape feathers rise above the height the of the head (Fig. 3C). In *niedda*, there is a foot stomp, but wings are not flicked open, and are only just raised slightly up-and-down over the back, which results in the cape flapping up, but not as high, and such that the terminal tips of the cape feathers stay at or below the level of the head (Fig. 4D).

If the pointing display does not transition into a bout of high intensity display (see below), the fore crown feathers may be pushed forward and back, which causes the



Figure 4 Pointing display of *niedda* as viewed by a female. The white arrow points to a female plumaged bird (and presumed female) observing the male on his display log. Note how the breast shield remains sleeked against the breast and is effectively invisible—its lateral tips concealed (shadowed) by the protruding “wings” of the cape. In this context, the eye-spots reflect so brightly relative to the super-black plumage of the rest of the male that they look like a pair of headlights “shining” toward the female. This “headlight pose” with the wing-like cape results in a very different appearance from the pointing display of *superba*. Image credit/source: Tim Laman/ML487540.

Full-size  DOI: [10.7717/peerj.4621/fig-4](https://doi.org/10.7717/peerj.4621/fig-4)

eye-spots to disappear and reappear or to “flash” on and off. In that scenario, the breast shield of *superba* is sometimes sleeked against the body again, which cause the reflective blue color to visually “blink off” as well. The cape-flapping may also revert into the pseudo wing-preen cape flicks that are a common feature of the advertisement display.

A noteworthy behavior associated with the initial display activity of *niedda* is a leaf tossing behavior (e.g., ML487565 from 1:24–1:35). For this behavior, the male picks up a leaf from the surface of the display log and tosses it into the air in such a way that it often lands on the log nearby. It is unclear if this behavior is a rudimentary form of court clearing behavior similar to that known from *Parotia* species or if it is some form of ritualized visual display like those of *Parotia carolae*, which uses leaves as props during certain displays (Scholes, 2006).

High intensity display

Our analysis identified one high intensity display in both species, which we call the cape presentation display. Our analysis did not uncover substantial variation in the behaviors,

postures and ornament forms among *s. superba*, *s. addenda* and *s. latipennis*, but did find minor variation in cadence of bouncing and snapping sounds (see below). As with the initial display activities, we use *s. latipennis* as the standard frame of reference for the *superba* complex and details on *s. superba* are provided in Fig. S1. As with the initial display activities above, our analysis of *niedda* found it to have numerous distinctive elements, which are described below.

Cape presentation display

The visual form and movements of this display comprise the quintessential features of courtship in the genus *Lophorina* (video vouchers: *superba* [ML458003](#); *niedda* [ML487557](#) and [ML487562](#)). When performed to a female, the cape presentation display is typically initiated from the posture of the pointing display—i.e., Fig. 3A *superba* and Figs. 3B and 4 *niedda*). However, if a female appears suddenly without stopping on a nearby perch on her approach, and during practice displays (no female present), the male will often transition directly into the cape presentation from any of initial display activities (e.g., in [ML487557](#) the pointing display is omitted and the male appears to be caught off guard by the sudden arrival of the female).

The cape presentation display begins when the male perceives a female making her approach toward the log. In both *superba* and *niedda*, the cape-flapping of the pointing display (see above) increases in intensity. In *niedda*, the increase is greater as wings are lifted higher over the back and then quickly flicked open and shut in the exaggerated manner of *superba* during pointing (Figs. 5A and 5B). As in the pointing of *superba*, the cape feathers of *niedda* also flap higher such that the tips exceed the height of the upward pointing bill (Fig. 5B). In conjunction with the exaggerated wing-flick/cape-flaps, the head is tilted back more sharply, the bill is also opened widely to reveal the bright yellow gape and the breast is thrust forward so that the feathers of breast shield ornament become fully expanded and conspicuous—its reflective surface angled upward toward the approaching female (Figs. 5A and 5B). The point at which the male presents his bright yellow gape is the best landmark for identifying of the start of the cape presentation display even though there is often a bout of the exaggerated wing-flick/cape-flaps preceding it.

The visual effect of the exaggerated wing-flick/cape-flaps with the breast shield fully revealed is more pronounced in *niedda* than *superba* because of the stark difference in the appearance of the breast shield during the pointing display (e.g., compare breast shield positions in Figs. 3A and 3B to those in Figs. 5A and 5B). In both species, the male will reorient himself as needed to track the position of the approaching female and keep his eye-spots and breast shield directed toward the female (e.g., video [ML487530](#)).

In *niedda*, bouts of wing-flick/cape-flapping coincide with a distinctive very rapid side-to-side wobbling of the head. As viewed from the front (i.e., the POV of the approaching female) the head wobbling has the effect of making the eye-spots flicker or shimmer. It is possible that the wobbling head movement may also be present in *superba*, but is not discernible from the available data.

Next comes the transition into the main part of cape presentation display—i.e., the presentation of the fully opened cape itself. In *superba*, the cape is lifted into its presentation



Figure 5 Cape presentation display of *superba* and *niedda*. The visual form of this display is the quintessential feature of courtship in the genus *Lophorina*. In both *superba* and *niedda* (A and B), cape-flapping increases in intensity. In *niedda* (B), the increase is greater because the wings are lifted higher over the back and then flicked open and shut in the exaggerated manner of *superba*. Simultaneously, the breast is thrust forward so that the breast shield becomes fully expanded and conspicuous with its reflective surface angled toward the approaching female. In *superba* (C), the cape is lifted into presentation position before to female arrives on the log. In *L. niedda* (D), wing-flick/cape-flaps continue for several more bouts after the female arrives and before the cape is put into presentation position. The appearance of the cape presentation phenotype differs dramatically between *superba* (E) and *niedda* (F). Image credit/source: (A, C and E) Edwin Scholes/ML458003, (B) Tim Laman/ML487538 (D and F) Tim Laman/ML487557.

Full-size DOI: 10.7717/peerj.4621/fig-5

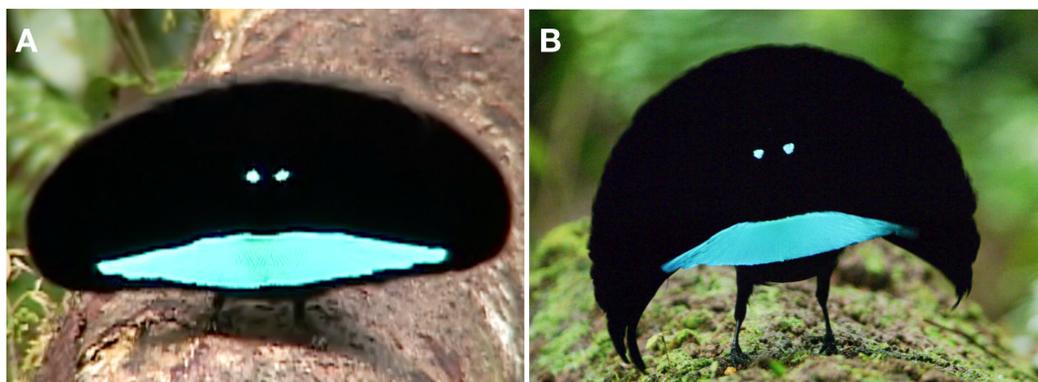


Figure 6 Detailed comparison of the cape presentation form of *superba* and *niedda*. In *superba* (A), the shape of the cape presentation form is oval—i.e., wider than it is high. The edge of the opened cape has a smooth fuzzy appearance, which is created by the distinct hair-like fringing along the terminal tips of the individual feathers that comprise the cape. In *niedda* (B), the shape of the cape presentation form is distinctly crescent shaped—i.e., it has a curved sickle shape that is broad in the center and tapers to a point at each end. The contour of the crescent is slightly ribbed and lacks the fuzzy appearance of *superba*. The shape and appearance of the breast shield also differs between the cape presentation phenotype of *superba* and *niedda*. In *superba* (A), the breast shield is wider with thicker terminal ends that make a relatively flat surface with a fairly straight edge along the top of the ornament. In *niedda* (B), the shorter and narrower terminal tips of the breast shield curve outward so that the surface of the ornament is slightly concave and the top edge is angled downward at the sides. This difference results in *niedda* looking like somewhat like “frowning face” whereas *superba* has more of a “smiling face” look. Also, the thinner profile of the narial tufts of *niedda* often makes the eye-spots look like they have thin blue “eyebrows” just above each eye-spots. Because the narial tufts of *superba* are shorter and do not extend over the top margin of the eye-spot, “eyebrows” are possible. Image credit/source: (A) Edwin Scholes/ML458003 and (B) Tim Laman/ML487563.

Full-size  DOI: 10.7717/peerj.4621/fig-6

position well before to female arrives on the log (Fig. 5C). In *L. niedda*, the wing-flick/cape-flaps with head wobbles continue for several more bouts after the female has arrived on the log and approaches the male become face-to-face with him (Fig. 5D). As the *niedda* female moves closer, the male will back up slightly and crouch lower before deploying his cape for full presentation (e.g., videos ML487530, ML487538, and ML487562).

Although the timing of cape deployment differs between *superba* and *niedda*, the cape of both is lifted into the full display position in largely the same way. First, it is spread wide, fan-like, over the back and then it is raised (anteriorly) and pushed over the head until it creates the super-black (McCoy *et al.*, 2018), slightly concave, cape presentation display form that surrounds the entire head and upper body (Figs. 5E & 5F and S1E).

Once in position however, the form and appearance of the cape presentation phenotype differs dramatically between *superba* and *niedda*. In *superba*, the shape of the cape presentation form is oval—i.e., wider than it is high (Figs. 6A & S1F). In comparison, the shape of the cape presentation form of *niedda* is distinctly crescent shaped—i.e., it has a curved sickle shape that is broad in the center and tapers to a point at each end (Fig. 6B). In *superba*, the border edge of the fully opened cape has a smooth fuzzy appearance (Fig. 6A), which is created by the distinct hair-like fringing along the terminal tips of the individual feathers that comprise the cape. The border edge of the crescent in *niedda* is slightly ribbed

and lacks the fuzzy appearance of *superba* (Fig. 6B). Correspondingly, the terminal tips of the *niedda* cape feathers have very minor hair-like fringing. The iconic oval shape of *superba* exhibits very little variation within the *superba* complex (e.g., Fig. 6A and Fig. S1F for a comparison of *L. s. latipennis* and *L. s. superba* and refer to the documentary films described in the Methods for comparative imagery of *L. s. addenda*).

The shape and appearance of the breast shield also differs between the cape presentation phenotype of *superba* and *niedda*. In *superba*, the breast shield is wider with thicker terminal ends that make a relatively flat surface with a fairly straight edge along the top of the ornament (Fig. 6A). In *niedda*, the shorter and narrower terminal tips of the breast shield curve outward so that the surface of the ornament is slightly concave and the top edge is angled downward at the sides (Fig. 6B). This difference results in *niedda* looking like somewhat like “frowning face” whereas *superba* has a “smiling face” look. The “smiling” vs “frowning” face appearance is further enhanced by the difference in how the eye-spot ornaments are created. In *superba*, the narial tufts are thick and relatively short whereas in *niedda* they are narrow and longer (i.e., extend beyond the width of the head). This difference has the effect of making the eye-spots of *niedda* appear smaller with a straighter line along the top edge, which gives the “eyes” the appearance of having slightly droopy “eyelids” compared with the always larger and circular appearance of the “eyes” in *superba* (Figs. 6A and 6B). In addition, when alignment of the feathers is not perfect relative to the viewer, the thinner profile of the narial tufts often makes the eye-spots of *niedda* look like they have a thin blue “eyebrow” just above each eye-spots (Fig. partially visible in Fig. 5F). Because the narial tufts for *superba* are shorter and do not extend over the top margin of the eye-spot, “eyebrows” are never visible nor even possible.

Throughout the cape presentation display, the transformed oval-shaped cape presentation form of *superba* is repeatedly lifted up and down, or bounced, with outstretched and bent legs (e.g., ML458003). The repeated up and down movements coincide with a series of alternating shuffle–hop steps to the side, which create the distinct bouncing cadence: up–down shuffle–hop, first to one side and then the other. When a female is present, the male’s bouncing shuffle–hop movements revolve around the female in either a semi-circular or full circle path.

In *niedda*, the overall appearance of the rotational movement during the cape presentation display is very different from that of *superba*. Instead of the characteristic bouncing of *superba*, the feet of *niedda* move in a faster, more pronounced, side-step motion without bouncing and with no visible up and down movement of the body. This creates the effect of *niedda* appearing to move in a quick but steady glide, rather than bounce, around the female in semi- or full circle (e.g., ML487557 and ML487562).

Along with the bouncing (*superba*) or smooth quick (*niedda*) rotational movement of the cape presentation form along the display log, the tail of both species is lifted to about 45 degrees above the plane of the back and rectrices are fanned. The secondary feathers of the wings are spread such that they become partially intertwined with the rectrices (see Fig. S1E). In one explosive motion, the wings are flicked open and shut to the sides, which causes a violent interaction among the secondaries and rectrices. In *superba*, the explosive wing-flicks occur rhythmically with the up–down bouncing movement and

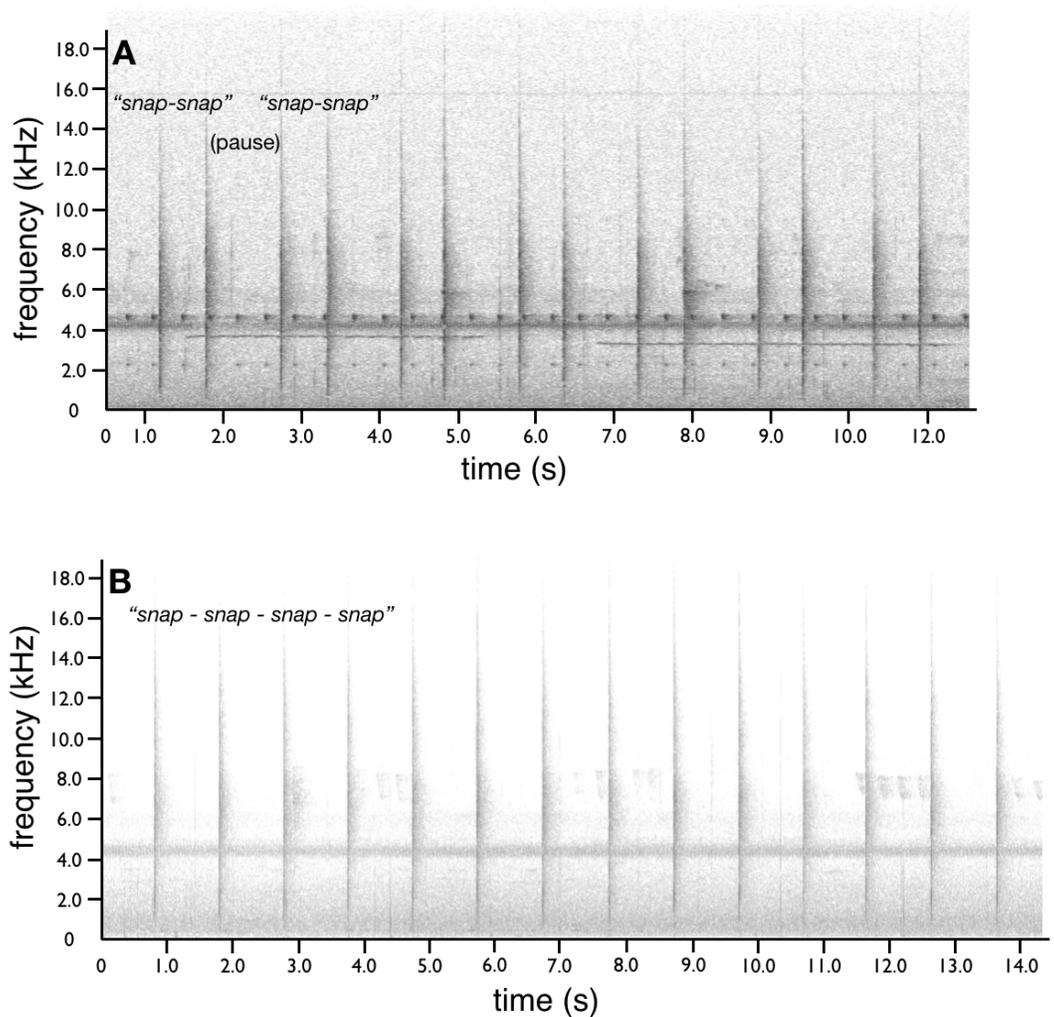


Figure 7 Wing-flick snaps of *superba* and *niedda*. In *superba* (A), distinct snapping sounds are a characteristic acoustic component of the cape presentation display and occur rhythmically with the up-down bouncing movement on the down beat of the bounces, but not on every bounce. In *superba latipennis*, the cadence of snaps and bouncing is down-snap-up, down-snap-up, down-up such that snaps occur in doublets with a distinct pause in between, which sounds like “snap-snap (pause) snap-snap”. In *niedda* (B), where the rotational movement lacks the bouncing of *superba*, the overall pattern and effect of the wing/tail flicks and snaps is very different because they occur at a regular interval that is not timed with any particular aspect of the rotational movement. The snaps of *niedda* are given at uniform beat of approximately one snap per second for a steady “snap-snap-snap” sound. Audio credit/source: (A) Edwin Scholes/ML458003 and (B) Edwin Scholes/ML8576351.

Full-size DOI: [10.7717/peerj.4621/fig-7](https://doi.org/10.7717/peerj.4621/fig-7)

coincides with the distinct snapping sounds that are a characteristic acoustic component of the display. In *superba*, the wing-flicks happen on the “down beat” of the bounces, but not on every bounce. In *s. latipennis*, the cadence of snaps and bouncing is down-snap-up, down-snap-up, down-up such that snaps occur in doublets with a distinct pause in between, which sounds like “snap-snap (pause) snap-snap” (Fig. 7A). In *niedda*, where the rotational movement lacks the bouncing of *superba*, the overall pattern and effect of the wing/tail

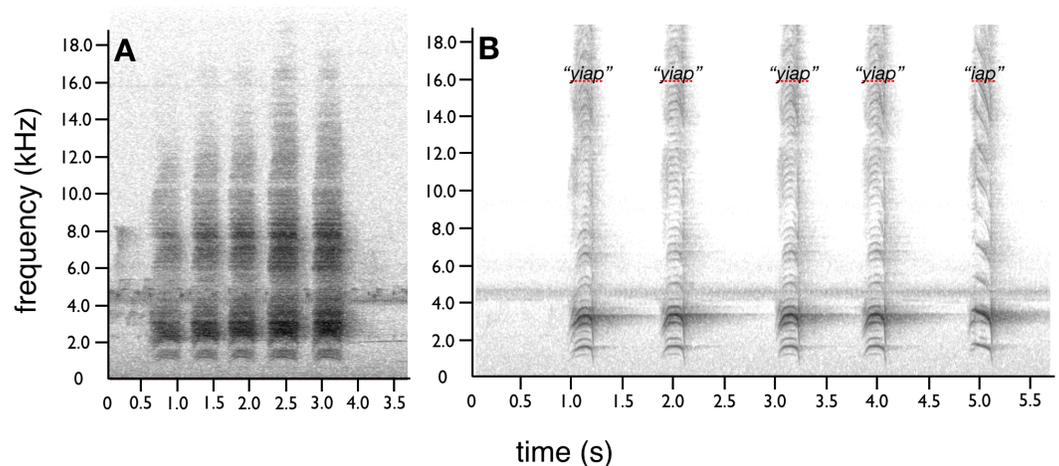


Figure 8 Advertisement vocalizations of *superba* and *niedda*. Advertisement vocalizations of both *niedda* and *superba* are phrases of 2–8 notes, with five notes common. While the number of notes is similar in both species, *superba* (A) gives a characteristic harsh raspy screech. The acoustic quality of *niedda* (B) vocalizations are very different. The basic note of *niedda* is a high-pitched nasal “yiap” sound, which has a piercing whistle-like quality that ascends and descends slightly in frequency. Audio credit/source: (A) Edwin Scholes/ML458003 and (B) Edwin Scholes/ML85763571.

Full-size  DOI: [10.7717/peerj.4621/fig-8](https://doi.org/10.7717/peerj.4621/fig-8)

flicks and snaps is very different because they occur at a regular interval that is not timed with any particular aspect of the rotational movement. The snaps of *niedda* are given at uniform beat of approximately one snap per second for a steady “snap-snap-snap” sound (Fig. 8B).

In *s. superba*, the cadence of the snapping is more frequent with less obvious choreography among the snaps and bouncing movements. In *s. addenda*, to the extent discernible from the documentary video sources, both the cadence of the bouncing and snapping seems to be more frequent with wing-flicks (and presumably the snaps) occurring with each downward bouncing stroke, “down-snap-up, down-snap-up, down-snap-up”. In both *niedda* and *superba*, the exact relationship between the wing movement and snapping sound production is unclear and warrants further investigation using high-speed videography.

In both *superba* and *niedda*, the cape presentation display ends when the female moves quickly away from the male such that he is unable to continue rotating around her, or when the female solicits copulation. At times the female moves along the log ahead of the male and at other times she will fly away from the log entirely. When females depart, males of both *superba* and *niedda* maintain the full cape presentation posture directed toward her and slowly lower it down over the back to readopt the pointing posture. In *niedda*, as the female departs, the male opens his bill to reveal the bright yellow gape once again. This end of display reveal of the gape was not observed in *superba*.

If a female solicits copulation (e.g., ML487568 from 0:07–0:17), she begins fluttering her wings as the male rotates around her and then will tip forward with breast low and tail high. At this point, the male circles closely and mounts the female while maintaining

the fully open cape posture. The cape is held in the open position during copulation and wing-snaps are given as part of, or just after, the wing flapping that occurs with copulation. After copulation, the male dismounts from the back of the female and resumes the cape presentation display directed at the female (e.g., [ML487562](#)). If she departs the log, the male holds the opened cape posture for a few seconds and then slowly lowers it and often returns to the pointing display and sometimes even reverts backwards through the entire sequence from pointing, to horizontal to advertisement displays.

Vocalizations

Advertisement vocalizations of both *niedda* and *superba* are phrases of 2–8 notes, with five notes being the most typical (video vouchers: *superba* [ML458003](#) and *niedda* [ML487530](#); audio voucher: *niedda* [ML85763571](#)). While the number of notes is similar in both species, the acoustic quality of *niedda* is very different from the characteristic harsh screeching notes of *superba* (Fig. 7). The basic note structure of *superba* is a harsh raspy screech with little acoustic structure (Fig. 7A). In comparison, the basic note of *niedda* is a high-pitched nasal “yiap” sound, which has a piercing whistle-like quality that ascends and descends slightly in frequency (Fig. 7B). Note that variation in *niedda* includes a version with a more constant pitch (i.e., the frequency does not ascend and/or descend), which sounds more like “yeep” instead of the up-and-down frequency of the “yiap” notes. Another common variant is slightly higher-pitched and distinctly descending to sound more like “iap” rather than “yiap” (Fig. 7B). While all three of the common note types can be present in a single phrase, they are usually not given that way. Phrases with a string of 5–6 “yiap” notes are the most common.

DISCUSSION

The primary purpose of this study was to provide the first description of the courtship phenotype of *Lophorina niedda* in the wild and determine if and how it differs from the courtship phenotype of *L. superba* with special consideration of what differences, if found, would mean in light of *niedda*'s newly recognized species status. A secondary goal was to provide a more thorough characterization of courtship phenotype diversity within the genus *Lophorina* in order to facilitate future in-depth comparative study.

Our results show that the *niedda* courtship phenotype differs from *superba* in numerous appearance, behavioral and acoustic components. Yet at the same time, the *niedda* courtship phenotype does not contain entirely unique courtship behaviors relative to *superba*—i.e., both have the same higher-order courtship phenotype architecture made up of three relatively simple initial display activities (advertisement, horizontal and pointing displays) and one complex high intensity display (cape presentation). In short, both *superba* and *niedda* share the same underlying courtship phenotype substructure, but differ in many details.

The six most diagnostic and noteworthy differences in the courtship phenotype of *niedda* compared with *superba* are: (1) the protruding wing-like position of the ornamental cape during the horizontal and pointing displays (Figs. 2B and 3B); (2) how the breast shield is obscured during the pointing display, which visually emphasizes the “headlight-like”

appearance of the eye-spot ornament as viewed by a female observer (Figs. 3 and 4); (3) how during the cape presentation display, the cape is not fully opened until *after* the female approaches at close range on the display log (Fig. 5D); (4) the striking difference in appearance of the fully opened cape presentation form—i.e., the distinctive crescent shape, the ribbed contour, the “frowning face” look of the breast shield and the way in which the eye-spots sometimes have “eyebrows” (Fig. 6); (5) how during the during of the cape presentation dance, the male revolves around the female with a smooth quick gliding motion (instead of the characteristic bouncing of *superba*) and with a constant (rather than doublet) wing-snap beat (Fig. 7); and (6) a piercing whistle-like vocalization instead of the characteristic raspy screech of *superba* (Fig. 8).

While the differences uncovered here are compelling, there are nevertheless several caveats to be considered. For example, our results are based on relatively low individual sample sizes for both *niedda* and *superba* and therefore may not reflect the full scope of intraspecific variation. However, with the basic framework now in place, future studies will be able to assess this more critically as larger sample sizes are obtained. It should also be noted that while we did not find substantial differences within *superba* (i.e., among *L. s. superba*, *L. s. addenda* and *L. s. latipennis*), sample sizes were limited, based on incomplete primary sources (for *L. s. addenda*) and included an outlying population from the Adelbert Mountains (*L. s. latipennis*) as the main frame of reference for all *superba*. To this last point, given the relatively small and geographically isolated population in the Adelbert Mountains, it is possible that further observations and larger sample sizes could reveal diagnostic differences between it (Adelbert) and cordillera populations. As noted in the Results, there are indications of differences in cadence of wing snaps and bouncing tempo of the cape presentation display among *L. s. superba*, *L. s. addenda* and *L. s. latipennis*. Quantifying these differences requires additional field observation and larger sample sizes.

What do the differences uncovered here mean with regard to the species status of *niedda*? We think the distinctive courtship phenotype confirms the conclusions of [Irestedt et al. \(2017\)](#) regarding the species status of *niedda*. With the mounting genetic, external morphological and now full courtship phenotype evidence, there can now be little doubt that population of *Lophorina* inhabiting the Bird’s Head Peninsula of western New Guinea is a distinct evolutionary lineage that is both geographically and reproductively isolated from the nearest population of *superba* in the Kobowre (Weyland) Mountains of the western cordillera. Furthermore, because all the differences described here are directly related to mating preferences of females and have likely evolved through divergent aesthetic preferences of females, it seems probable that *niedda* and/or *superba* females would not find males of the other type as attractive as males of their own type. However, reciprocal exclusivity in female mating preferences is not required to meet the standards of species delineation in the birds-of-paradise. With the exception of the newly defined *L. minor*, for which there is not enough data to make a determination, bird-of-paradise species are defined by the degree of differences in their courtship phenotypes. In other words, courtship phenotype disparity is the key criterion for species diagnosis in the birds-of-paradise. By this yardstick, *L. niedda* is clearly a distinct species.

In addition to characterizing the courtship phenotype of *niedda* for the first time, our results also provide a more complete picture of the *superba* courtship phenotype. For the first time, we document that the initial display activity of *superba* is comprised of three distinct behaviors: the advertisement, horizontal and pointing displays (Figs. 1–3). Previous efforts to describe the displays of *superba* did not differentiate these components into distinct displays even though the basic patterns were described (Frith & Beehler, 1998). We also provide the most detailed (and vouchered) descriptions of the *superba* courtship phenotype to date.

The findings presented here, along with those of Irestedt et al. (2017) indicating that *L. minor* is the most genetically divergent lineage in the genus, highlight the need for more investigation of the courtship phenotype of *minor*. Are there differences in the courtship phenotype of *minor* that would shed light on its species status? Currently the only information about the courtship behavior of *minor* comes from incomplete observations of a single captive male that housed in the London Zoological Gardens during the late 1920's and mid 1930's (Manson-Bahr, 1935; Morrison-Scott, 1936; Seth-Smith, 1936). While lacking sufficient description to be fully comparable to the data presented here, it is nevertheless possible to glean several key details. For one, it is evident that *minor* does perform the cape presentation display. However, the presence/absence of initial display activities is unclear from the available data. In fact, when describing the cape presentation display, Manson-Bahr goes as far as stating, “there are no preliminary stages... the display is spontaneous and instantaneous” (Manson-Bahr, 1935, pg. 67). While undoubtedly possible, we feel fairly confident that some form of these initial behaviors were either overlooked or lacking by virtue of the conditions of captivity. Regarding the cape presentation display, it is clear from both written descriptions and illustrations that the form of the cape presentation is oval-shaped like *superba*, not crescent-shaped like *niedda*, with visible eye-spots made by the crown feathers (Morrison-Scott, 1936; Seth-Smith, 1936). The captive *minor* also performed movements that were consistent with the bouncing motions that are characteristic of *superba* during its cape presentation dances (Morrison-Scott, 1936). The displays of the captive also included apparent wing movement that produced “clicking” noises (Morrison-Scott, 1936). The only possibility of a distinct difference from *superba* that is evident in the descriptions of the captive *minor* is a very clear description of how the eye-spot ornaments have small black spots in their centers, which have the effect of looking like pupils (Morrison-Scott, 1936). It was hypothesized that the “pupils” were created through a concave surface to the feathers that create the eye-spots, which seems plausible. However, solid conclusions about the courtship phenotype of *minor* will have to await future field study.

CONCLUSIONS

Given the substantial differences in so many aspects of the *niedda* courtship phenotype combined with the acute geographic isolation of *niedda* populations from *superba* populations, leaves little doubt that *niedda* deserves full species status as proposed by Irestedt et al. (2017).

The species validity *niedda* underscores the importance of Indonesian New Guinea's Bird's Head and Bird's Neck eco-regions (i.e., the Vogelkop Peninsula) as a center of endemic biodiversity that deserves particular attention from the conservation community. Among birds-of-paradise alone, *L. niedda* now joins the three other montane species endemic to the region (*Astrapia nigra*, *Paradigalla longicuda*, and *Parotia sefilata*) and opens the door for additional systematic scrutiny of the entire avifauna of the Bird's Head (Vogeklop) region, including the other birds-of-paradise at middle and upper elevations (e.g., *Drepanonris albertisi* and *Epimachus fastosus*). Given that the Bird's Head region was the first part of New Guinea to be ornithologically explored, and discovery of new species of birds-of-paradise was the main driver of exploration, it is surprising that the distinctive features of the *niedda* courtship phenotype, and therefore the species status of this unique population, have remained elusive for so long. Yet this fact underscores the need for continued exploration of New Guinea's forests and further systematic investigation of all taxa, including those like the avifauna which are often considered to be relatively well known.

ACKNOWLEDGEMENTS

For field support and logistics we thank Shita Prativi, Benny Mambrasar and Jordan Mencher of Magnificus Expeditions and Papua Konservasi dan Komunitas. We offer sincere thanks to Pak Desa and the people of Minggre Village for granting access to their land, for being generous hosts and for excellent assistance in the field. We thank the Provincial Government of West Papua and Professor Charlie Heatubun, Head of the Research and Development Agency, for supporting of research and conservation in West Papua. Brad Walker, Matt Medler, Karen Rodriguez and Rick Elliker from the Cornell Lab of Ornithology provided critical support with multimedia data archival in the Macaulay Library. Bruce Beehler and an anonymous reviewer made valuable comments, which greatly improved the manuscript.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

This work was supported by the Cornell Lab of Ornithology. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
Cornell Lab of Ornithology.

Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Edwin Scholes conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Timothy G. Laman conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.

Data Availability

The following information was supplied regarding data availability:

Macaulay Library at the Cornell Lab of Ornithology

Accession #: [ITM89474](https://doi.org/10.1111/j.1096-0031.1992.tb00049.x).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.4621#supplemental-information>.

REFERENCES

- Beehler BM, Pratt TK. 2016.** *Birds of new guinea: distribution, taxonomy, and systematics*. Princeton: Princeton University Press.
- Bostwick KS, Harvey TA, Scholes III E. 2017.** Leveraging diverse specimen types to integrate behavior and morphology. In: Webster MS, ed. *The extended specimen: emerging frontiers in collections-based ornithological research*. Boca Raton: CRC Press.
- Cracraft J. 1992.** The species of the birds-of-paradise (Paradisaeidae): applying the phylogenetic species concept to a complex pattern of diversification. *Cladistics* 8:1–43 DOI [10.1111/j.1096-0031.1992.tb00049.x](https://doi.org/10.1111/j.1096-0031.1992.tb00049.x).
- Frith CB, Beehler B. 1998.** *The birds of paradise: Paradisaeidae*. Oxford: Oxford University Press.
- Frith DW, Frith CB. 1988.** Courtship display and mating of the Superb Bird of Paradise *Lophorina superba*. *Emu* 88:183–188 DOI [10.1071/MU9880183](https://doi.org/10.1071/MU9880183).
- Frith CB, Frith DW. 2009.** Paradisaeidae (birds of paradise). In: Del Hoyo J, Elliott A, Christie D, eds. *Handbook of the birds of the world*. Vol. 14. Barcelona: Lynx Edicions, 404–492.
- Irestedt M, Batalha-Filho H, Ericson P, Christidis L, Schodde R. 2017.** Phylogeny, biogeography and taxonomic consequences in a bird-of-paradise species complex, *Lophorina-Ptiloris* (Aves: Paradisaeidae). *Zoological Journal of the Linnean Society* 181(2):439–470.
- Laman T, Scholes E. 2012.** *Birds of paradise: revealing the world's most extraordinary birds*. Washington, D.C.: National Geographic Books.
- Manson-Bahr PH. 1935.** Remarks on the displays of birds of paradise. *Bulletin of the British Ornithological Club* 56:63–68.

- McCoy D, Feo T, Harvey TA, Prum RO. 2018.** Structural absorption by barbule microstructures of super black bird of paradise feathers. *Nature Communications* **9**(1):1–8 DOI [10.1038/s41467-017-02088-w](https://doi.org/10.1038/s41467-017-02088-w).
- Morrison-Scott T. 1936.** Displays of *Lophorina superba* minor. *Proceedings of the Zoological Society London* **1336**:809.
- Pratt TK, Beehler BM. 2015.** *Birds of New Guinea*. Second Edition. Princeton: Princeton University Press.
- Scholes E. 2006.** Courtship ethology of Carola's Parotia (*Parotia carolae*). *The Auk* **123**(4):967–990.
- Scholes E. 2008a.** Evolution of the courtship phenotype in the bird of paradise genus *Parotia* (Aves: Paradisaeidae): homology, phylogeny and modularity. *Biological Journal of the Linnean Society* **94**:491–504 DOI [10.1111/j.1095-8312.2008.01012.x](https://doi.org/10.1111/j.1095-8312.2008.01012.x).
- Scholes E. 2008b.** Structure and composition of the courtship phenotype in the bird of paradise *Parotia lawesii* (Aves: Paradisaeidae). *Zoology* **111**:260–278 DOI [10.1016/j.zool.2007.07.012](https://doi.org/10.1016/j.zool.2007.07.012).
- Scholes E, Beehler BM, Laman T. 2017.** Taxonomic status of *Parotia berlepschi* Klein-schmidt, 1897 based on analysis of external appearance, voice and behavior (Aves: Paradisaeidae). *Zootaxa* **4329**(6):560–572 DOI [10.11646/zootaxa.4329.6.2](https://doi.org/10.11646/zootaxa.4329.6.2).
- Scholes E, Gillis J, Laman TG. 2017.** Visual and acoustic components of courtship in the bird-of-paradise genus *Astrapia* (Aves: Paradisaeidae). *PeerJ* **5**:e3987 DOI [10.7717/peerj.3987](https://doi.org/10.7717/peerj.3987).
- Seth-Smith D. 1936.** Remarks on the display of Birds of Paradise. *Proceedings of the Zoological Society of London* **1936**:807–808.
- Timmis WH. 1968.** Breeding of the superb bird of paradise at the chester zoo. *Avicultural Magazine* **74**:170–172.
- Whiteside R, Feignan M. 1998.** Displays and associated behavior of wild Superb Birds of Paradise *Lophorina superba*. *Australian Bird Watcher* **17**:357–363.